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Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation

H. P. Linder[1,*], Caroline E. R. Lehmann[2,3], Sally Archibald[3], Colin P. Osborne[4] and David M. Richardson[5]

[1] *Department of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, CH 8008 Zurich, Switzerland*
[2] *School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, UK*
[3] *Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, Private Bag X3, WITS, 2050, South Africa*
[4] *Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K.*
[5] *Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa*

ABSTRACT

Poaceae (the grasses) is arguably the most successful plant family, in terms of its global occurrence in (almost) all ecosystems with angiosperms, its ecological dominance in many ecosystems, and high species richness. We suggest that the success of grasses is best understood in context of their capacity to colonize, persist, and transform environments (the "Viking syndrome"). This results from combining effective long-distance dispersal, efficacious establishment biology, ecological flexibility, resilience to disturbance and the capacity to modify environments by changing the nature of fire and mammalian herbivory. We identify a diverse set of functional traits linked to dispersal, establishment and competitive abilities. Enhanced long-distance dispersal is determined by anemochory, epizoochory and endozoochory and is facilitated *via* the spikelet (and especially the awned lemma) which functions as the dispersal unit. Establishment success could be a consequence of the precocious embryo and large starch reserves, which may underpin the extremely short generation times in grasses. Post-establishment genetic bottlenecks may be mitigated by wind pollination and the widespread occurrence of polyploidy, in combination with gametic self-incompatibility. The ecological competitiveness of grasses is corroborated by their dominance across the range of environmental extremes tolerated by angiosperms, facilitated by both C_3 and C_4 photosynthesis, well-developed frost tolerance in several clades, and a sympodial growth form that enabled the evolution of both annual and long-lived life forms. Finally, absence of investment in wood (except in bamboos), and the presence of persistent buds at or below ground level, provides tolerance of repeated defoliation (whether by fire, frost, drought or herbivores). Biotic modification of environments *via* feedbacks with herbivory or fire reinforce grass dominance leading to open ecosystems. Grasses can be both palatable and productive, fostering high biomass and diversity of mammalian herbivores. Many grasses have a suite of architectural and functional traits that facilitate frequent fire, including a tufted growth form, and tannin-like substances in leaves which slow decomposition. We mapped these traits over the phylogeny of the Poales, spanning the grasses and their relatives, and demonstrated the accumulation of traits since monocots originated in the mid-Cretaceous. Although the sympodial growth form is a monocot trait, tillering resulting in the tufted growth form most likely evolved within the grasses. Similarly, although an ovary apparently constructed of a single carpel evolved in the most recent grass ancestor, spikelets and the awned lemma dispersal units evolved within the grasses. Frost tolerance and C_4 photosynthesis evolved relatively late (late Palaeogene), and the last significant trait to evolve was probably the production of tannins, associated with pyrophytic savannas. This fits palaeobotanical data, suggesting several phases in the grass success story: from a late Cretaceous origin, to occasional tropical grassland patches in the later Palaeogene, to extensive C_3 grassy woodlands in the early–middle Miocene, to the dramatic expansion of the tropical C_4 grass savannas and grasslands in the Pliocene, and the C_3 steppe grasslands

* Address for correspondence (Tel: +41 (44) 634 8410; E-mail: peter.linder@systbot.uzh.ch).

during the Pleistocene glacial periods. Modern grasslands depend heavily on strongly seasonal climates, making them sensitive to climate change.

Key words: biological invasions, Gramineae, grassland, macro-evolution, Poaceae, savanna.

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I. INTRODUCTION

Grasses (Gramineae, Poaceae) are the modern world's most successful angiosperm family. Ecosystems dominated by grasses cover 31–43% of the land surface (Gibson, 2009) and, although grasses account for only 3% of plant species on Earth, grass-dominated landscapes contribute 33% of global primary productivity, compared to the 48% by forests (Beer *et al.*, 2010). Indeed, net primary productivity of grass-dominated ecosystems can equal or exceed that of adjacent forested ecosystems, as can their soil carbon stores (Oliveras *et al.*, 2014). Grasses occupy ecosystems ranging from the driest [*Stipagrostis zitellii* (Asch.) De Winter in the hyperarid Sahara (J. Léonard in White, 1983)] to the coldest (*Deschampsia antarctica* E.Desv. is one of the two angiosperms on Antarctica) environments on Earth, and from sun-drenched savannas to the dark understorey of tropical rainforest [e.g. *Oplismenus burmannii* (Retz.) P.Beauv.] (Fig. 1).

Over deep time, the evolution of grasses and the expansion of the biomes in which they dominate have transformed the biosphere. In the early to middle Miocene, grasses using the C_3 photosynthetic pathway displaced temperate forests, and in the late Miocene grasses using the derived C_4 photosynthetic pathway displaced tropical forests, shrublands and C_3 grasslands (Edwards & Smith, 2010). These novel ecosystems precipitated major floral and faunal radiations (Jacobs, Kingston & Jacobs, 1999; Owen-Smith, 2013), and a global increase in the frequency of fire (Keeley & Rundel, 2005). Indeed, the prevalence of fire and mammalian herbivory in grass-dominated ecosystems has global impacts on the silica (Kidder & Gierlowski-Kordesch, 2005), carbon (Pagani *et al.*, 2009; van der Werf *et al.*, 2010) and nitrogen (Chen *et al.*, 2010) cycles, and may influence local water availability (Honda & Durigan, 2016). Bipedalism evolved and hominin species diversified in grasslands and savannas (Bonnefille, 2010). An extensive fauna now depends on grasses and grass-dominated biomes (McNaughton *et al.*, 1989), and grassy vegetation is significantly exploited as forage for livestock and covers important catchments for water provision. Globally, 60% of human energy intake is derived from three cereal species (wheat, rice, maize; FAO, 1995) domesticated ~9000–10000 years ago from wild annual grasses (Purugganan & Fuller, 2009). By all measures, grasses have a significant and arguably disproportionate impact on global ecology, biogeochemical cycles and human subsistence.

The grasses are, with approximately 11000 species (Clayton *et al.*, 2015), the fifth most species-rich angiosperm family. Poaceae have twice the number of species as the next largest wind-pollinated family, Cyperaceae, which has approximately 5000 species. In fact, grasses account

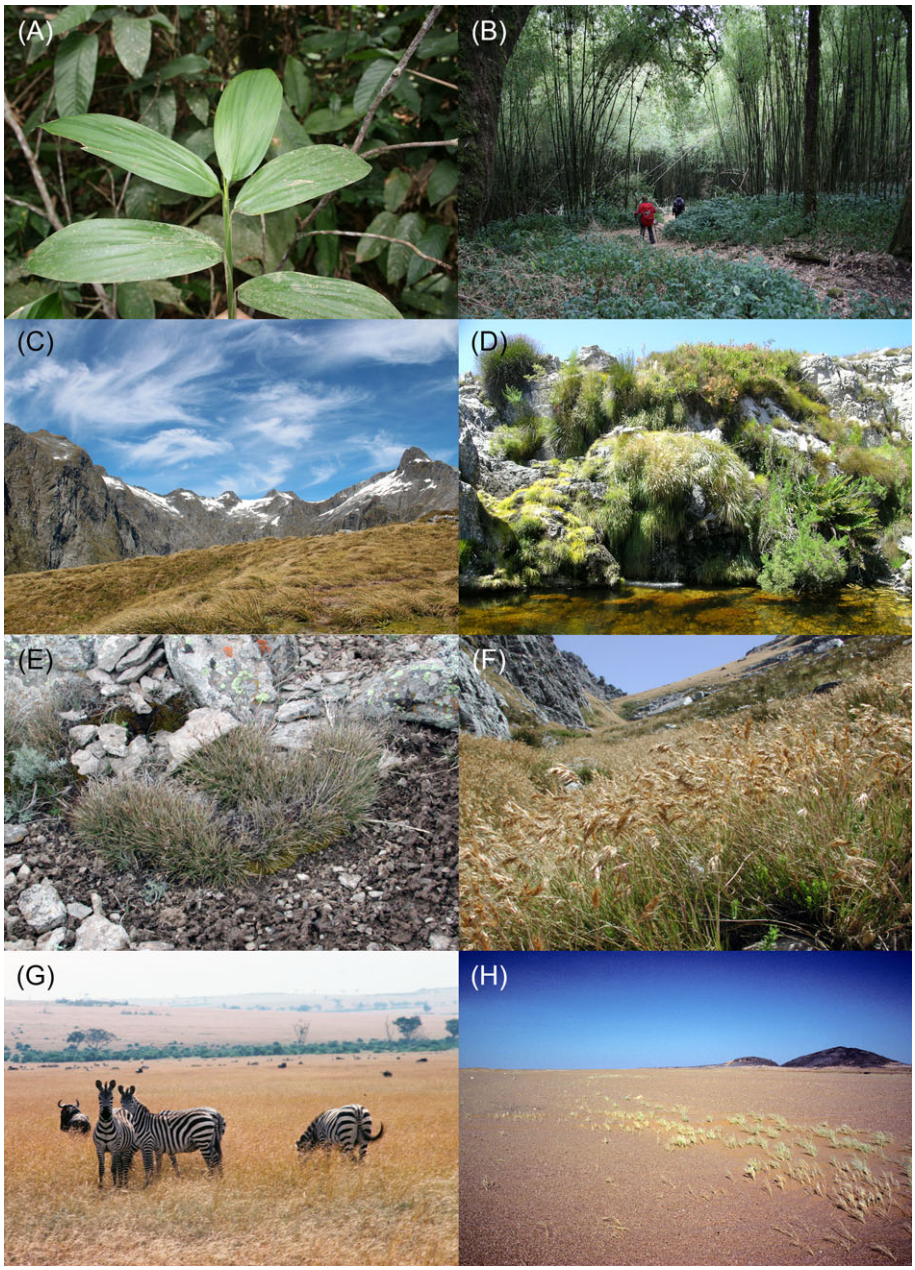

Fig. 1. Diverse grass habitats. (A) *Olyra latifolia* in Cameroonian forest understorey; (B) *Arundinaria alpina* thicket in Cameroon; (C) alpine *Chionochloa* in New Zealand; (D) *Pentameris capensis* in a permanent stream, South Africa; (E) *Pentameris minor* at 4000 m in the Bale mountains, Ethiopia; (F) *Pentameris oreophila* in the mountains of the Western Cape, South Africa; (G) zebra in the Masai Mara savanna, Kenya; (H) *Stipa* in the Sahara, south of Tamanrasset, Algeria. All photos: H.P. Linder.

for more than 30% of all wind-pollinated angiosperm species (Linder, 1998). The immediate sister families to Poaceae are very species poor: Ecdeiocoleaceae comprises just two species, Joinvilleaceae just four species, and the restiid clade (Restionaceae, Anarthriaceae) some 550 species. Sister to pooids (Poaceae, Ecdeiocoleae, Joinvilleaceae) and restiids (Restionaceae, Anarthriaceae) is Flagellariaceae with only five species (Wepfer & Linder, 2014). In the grasses, the basal lineages [Anomochlooideae, Pharoideae and Puellioideae (GPWG, 2001; Kellogg, 2015; Soreng *et al.*, 2015)] are also species poor, and the major acceleration of the diversification in Poaceae only occurred in the Bambusoideae–Ehrhartoideae–Pooideae (BEP) and Panicoideae–Arundinoideae–Chloridoideae–Micrairoideae–Aristidoideae–Danthonioideae (PACMAD) clades (Linder & Rudall, 2005; Spriggs, Christin & Edwards, 2014).

Poaceae is an old clade, and modern dominance of grasses was likely achieved stepwise through the Cenozoic [the last 65 million years (Myr)]. The presence of putative

grass phytoliths in dinosaur coprolites (Prasad *et al.*, 2005) suggests a late Cretaceous stem age [70–80 million years ago (Ma)] if interpreted as generalized grass, rather than as oryzoid, phytoliths. Most fossil-calibrated molecular clocks corroborate this (Bouchenak-Khelladi, Muthama & Linder, 2014*;* Christin *et al.*, 2014), but Magallón *et al.* (2015) found a Palaeocene stem age (*c.* 52 Ma). As fossil evidence suggests grasses were widespread by the end of the Cretaceous, and that the first grazers may have evolved by then (Strömberg, 2011), we here follow the Cretaceous origin of the grasses. These early grass lineages probably diversified in the tropical forest understorey, or at least under tree canopies (Clayton, 1981; Strömberg, 2011). At the latest in the Eocene (56–34 Ma) and during the Oligocene (34–23 Ma) grasses were a significant proportion of the Southeast Asian West Natuna Basin (Morley, Morley & Restrepo-Pace, 2003), as well as along the West African Nigerian coast (Morley, 2000) floras. This indicates at least the presence of grass, but possibly also grassy patches, leading Strömberg (2011) to suggest that by the end of the Eocene grasses had a global distribution and the first open-habitat grasslands had established.

From the Miocene (23–5.3 Ma) there is increasing evidence for extensive grassy vegetation (Strömberg, 2011). Detailed analyses of phytoliths from North America (Strömberg, 2005) and Turkey (Strömberg *et al.*, 2007) indicate these grasslands were C_3 dominated. There are some indications that the North and South American open grasslands were established by the earliest Oligocene; however, there is more convincing evidence of their presence in the mid-Miocene (Jacobs *et al.*, 1999; Strömberg, 2011). Open woodland and grassy patches may have been present in Africa from the Eocene (Morley, 2000), but the evidence for grasslands in Eurasia before the Miocene is tenuous (Jacobs *et al.*, 1999). In the Late Miocene–Pliocene these C_3 grasslands were replaced by C_4 grasses in tropical regions (Edwards *et al.*, 2010; Feakins *et al.*, 2013; Hoetzel *et al.*, 2013; Uno *et al.*, 2016), resulting in the establishment of extensive grasslands across the tropics. In Africa these C_4-dominated savanna systems were established after the diversification of woody plants with spiny defences against ungulate browsers (Charles-Dominique *et al.*, 2016), but before the Pleistocene (2.6–0.01 Ma) origins of geoxylic trees (Maurin *et al.*, 2014). Simplistically, grasses seem to have evolved, in several distinct steps, from relatively unimportant forest-understorey plants, to grassy patches by the end of the Palaeogene, to mixed tree–grass systems with an early associated fauna by the early Miocene, to globally distributed fire-associated savannas and steppe grasslands with a distinct grazing fauna (Owen-Smith, 2013) by the Pliocene (Jacobs *et al.*, 1999).

Currently, grasses are species rich, occur in almost all habitats with angiosperms, and in many ecosystems grasses are not only dominant, but substantially influence the environment *via* major impacts on co-occurring animal species and the flammability of landscapes (Archibald *et al.*, 2013). The extent of grass-dominated vegetation influences regional climates, hydrology, nutrient cycling and numerous ecosystem functions. Yet, although the reasons for the success of the C_4 grass-dominated savannas have been repeatedly explored (see, for example, Edwards *et al.*, 2010; Bouchenak-Khelladi *et al.*, 2014; Estep *et al.*, 2014), reasons for the success and global significance of Poaceae (both in C_4 savannas and C_3 steppe grasslands) have not been clearly elucidated. The currently dominant paradigm is that success, in all eukaryotes, is a result of adaptive radiations (Simpson, 1953; Wiens, 2017). However, here we argue that the success of grasses is rooted in their invasive ability. We term this the 'Viking Syndrome', because Vikings were highly successful raiders from the 9th to the 11th centuries, raiding from North America to North Africa, from the White Sea to the Caspian Sea. In several regions they established colonies which grew into new states and transformed the political landscape, for example in Normandy, England (the Norman conquest under William the Conqueror), Sicily and southern Italy, and Russia (the Rus was a Viking group, after whom Russia was named, and the Romanovs were descended). The Viking Syndrome postulates success due to efficient dispersal, rapid population growth, resilience to disturbance, phenotypic plasticity and the ability to transform environments to benefit the invader. Not only do grasses disperse across oceans and continents, but they are also able to rapidly establish persistent populations, and diversify in new and disparate environments. Possibly most important, dominance by grasses often results in environmental transformation *via* altered fire and herbivory regimes, which in turn reinforces grass dominance by acting as an environmental filter which excludes species which otherwise might out-compete them. Today, grasses are one of the most successful groups in terms of biological invasions (Fig. 2), and recent invasions in many parts of the world have highlighted their capacity to transform environments (e.g. D'Antonio & Vitousek, 1992; Gaertner *et al.*, 2014). We suggest that the characters defining grasses as invasive species in a contemporary context are the same as those that enabled grasses to colonize, dominate, and transform large portions of the Earth's surface over the last 10–20 Myr. We propose four functional attributes that make the grasses such effective invaders: (*i*) dispersal ability, which means that they can reach all continents. This is illustrated by the occurrence of cosmopolitan grass species, such as *Deschampsia cespitosa* (L.) P.Beauv., *Cynodon dactylon* (L.) Pers. and *Heteropogon contortus* (L.) P.Beauv. (*ii*) Establishment ability, which allows immigrants to rapidly establish populations and become ecologically dominant (e.g. Levick *et al.*, 2015). (*iii*) Phenotypic plasticity and evolutionary lability, which enable grasses to occupy a diversity of environments and maintain viable populations. (*iv*) Generation and tolerance of chronic disturbance, specifically fire and herbivores, which enable grasses to persist in environments where these disturbances limit the growth of woody plants.

We first present evidence that the grasses are indeed excellent colonizers, using data from both the Anthropocene and earlier. Then we discuss the traits that may confer this functional competence on the grasses, and show that

Fig. 2. Examples of palaeo- (A, B) and anthropogenic (C–F) grass invasions. (A) *Acacia* (*Vachelia*) *nilotica* being burnt in a *Bothriochloa insculpta* savanna grassland. (B) Andropogonoid savanna grassland in the Kruger National Park, South Africa. (C) Red snowtussock grass (*Chionochloa rubra*) expansion following human disturbance in New Zealand. (D) Gamba grass (*Andropogon gayanus*) in Australia's Northern Territory. (E) *Pennisetum setaceum* invasion on Hawaii. (F) Buffel grass (*Cenchrus ciliaris*) invasion in Arizona, USA. Photo credits: (A) S. Archibald; (B, C) H.P. Linder; (D) D.M. Richardson; (E) J.J. Le Roux; (F) J.L. Betancourt.

their success is in relation to the number of these functions they perform effectively. Finally, we show in a phylogenetic context how these traits accumulated during the evolutionary history of the grasses, resulting in the super-plants of the later Neogene.

II. EVIDENCE OF GRASSES BEING INVASIVE

The evidence that grasses are, and have been, highly invasive can be grouped into two sets of observations. The first are the human-mediated (Anthropocene) invasions, which show the ability of a lineage to naturalize (i.e. establish self-sustaining populations) and become invasive (i.e. spread from introduction sites) where humans have fast-tracked dispersal between biogeographic zones. This contrasts with pre-human range expansions (palaeo-invasions), which arose from a combination of natural long-distance dispersal and establishment capacity. Consequently, important traits in Anthropocene invasions relate to colonization and competitive ability, whereas in the palaeo-invasions traits that facilitate dispersal are added to the mix.

(1) Anthropocene invasions

Anthropocene grass invasions (Fig. 2) are widespread, and have significant impacts both on resource availability and local disturbance regimes (D'Antonio & Vitousek, 1992). Indeed, among invaders of natural areas, Poaceae, along with Fabaceae and Hydrocharitaceae, are overrepresented (Daehler, 1998). This is not surprising, as grasses, due to their economic importance, have been widely translocated by humans; for example, more than 2200 grass species have been introduced to Australia since European colonization. Indeed, the only family with more introduced species in Australia is Fabaceae (Cook & Dias, 2006). Many species were widely planted, providing substantial propagule pressure for launching invasions, and many species have been introduced multiple times – both factors are well known as

Table 1. Frequency of grasses (Poaceae) in global and regional lists of invasive alien species. Regions are ordered by size. The lists used here vary in their comprehensiveness, in the criteria used for labelling species as invasive, and whether the species are spreading only in (semi)natural or in all habitats

List name (organization or source)	Region	Area (million km[a])	% grasses
100 of the World's Worst Invasive Alien Species (IUCN)[b]	Global		6
59 of the 'worst invasive plants in protected areas of the world' (Foxcroft *et al.*, 2017)	Global		12
State Noxious Weeds (USA) (http://www.invasive.org)	USA	9.83	14
32 'Weeds of National Significance'; (http://www.environment.gov.au/biodiversity/invasive/weeds/weeds/lists/wons.html)	Australia	7.69	9
Northern Territory Government Weed Risk Management System (Rossiter-Rachor *et al.*, 2013)[a]	Northern Territory, Australia	1.42	31
Pretoria National Herbarium/BRAHMS[c]	South Africa	1.22	11
The Jepson Manual: Vascular Plants of California, 2nd edn. (Baldwin *et al.*, 2012)[d]	California, USA	0.42	25–27
Plantas invasores en Cuba (Regalado *et al.*, 2012)[e]	Cuba	0.11	16
Consolidated list of environmental weeds in New Zealand (Howell, 2008)	New Zealand	0.27	13
Catalogue of alien plants of the Czech Republic (2nd Ed.) (Pyšek *et al.*, 2012)	Czech Republic	0.08	7
List of transformer plant species (Trueman, 2009)[f]	Galapagos Islands	0.01	23
Invasive plants species of La Reunion Island, Western Indian Ocean (http://www.especesinvasives.re)[g]	La Reunion	0.002	10
Invasive alien flora of Jhabua district, Madhya Pradesh, India (Wagh & Jain, 2015)	Jhabua district, Madhya Pradesh, India	0.004	5

[a]Grasses comprised 17 out of 55 plant species scored as High or Very High in the Northern Territory Government Weed Risk Management System (database accessed 19 May 2017).
[b]Two out of 32 land plants.
[c]Out of 1050 naturalized alien taxa for South Africa, excluding taxa known in the country for <10 years (L. Henderson, personal communication, May 2017).
[d]173 alien grass species are conclusively invasive in CA, out of a total of 650–700 invasive vascular plant species.
[e]Grasses comprise 13% of all environmental weeds.
[f]52 species out of 322 are grasses, but the authors mention "many taxonomic issues" when listing grass taxa.
[g]13 out of 130 species of invasive vascular plant species in native habitats (accessed 7 May 2017).

major promoters of invasiveness (Hui & Richardson, 2017). Grasses have thus had excellent opportunities to become aggressive invaders, and their biology has enabled them to capitalize on these opportunities.

There is no critical listing of how many species (thus which proportion) of grasses have become naturalized or invasive following introduction to new regions. Such data are available for some other growth forms, such as trees and shrubs. Among woody plants, Pinaceae has the highest proportion of invasive species, with 12% classified as invasive (Richardson & Rejmanek, 2004). Collating such data is more difficult for grasses as introduction histories and lists of naturalized/invasive species are generally very poor for most regions (except South Africa, see Visser *et al.*, 2016, 2017).

Grasses are over-represented among invasive taxa (Table 1), whether it be as 6% of the plants among "100 worst invasive alien species" or seven of 59 "worst invasive plants in protected areas of the world" (Foxcroft *et al.*, 2017). Further, grass invasions are recognized to have dramatic impacts on ecosystem ecology, *via* alterations of fuel properties and fire regimes (D'Antonio & Vitousek, 1992), or altering nutrient cycling (Pellegrini, Hoffmann & Franco, 2014) that may bring about regime shifts that transform ecosystem functions and processes (D'Antonio & Vitousek, 1992; Brooks *et al.*, 2004; Gaertner *et al.*, 2014).

Grass species may also undergo rapid range expansions within a biogeographic region. For example, in New Zealand, human arrival and consequent increases in fire frequency led to the replacement of fire-sensitive forests and shrublands with indigenous pooid species (*Poa*, *Festuca*, *Elymus*), later replaced by native *Chionochloa* grass species (McGlone, 2001). These examples illustrate grasses as competent, aggressive invaders with the capacity to transform ecosystems over decades and over environmental gradients.

(2) Palaeo-invasions

The hypothesis that grasses were 'invasive' before the Anthropocene ('palaeo-invasions' *sensu* Richardson *et al.*, 2000) is based on three lines of evidence. Firstly, historical biogeographical analyses of specific clades demonstrated frequent inter-continental dispersal and establishment, followed by adaptation and radiation on new continents. Secondly, the rapid Neogene (23–2.6 Ma) spread of C_4 grass clades transformed biotic environments *via* novel ecological pressures and consequent species radiations in

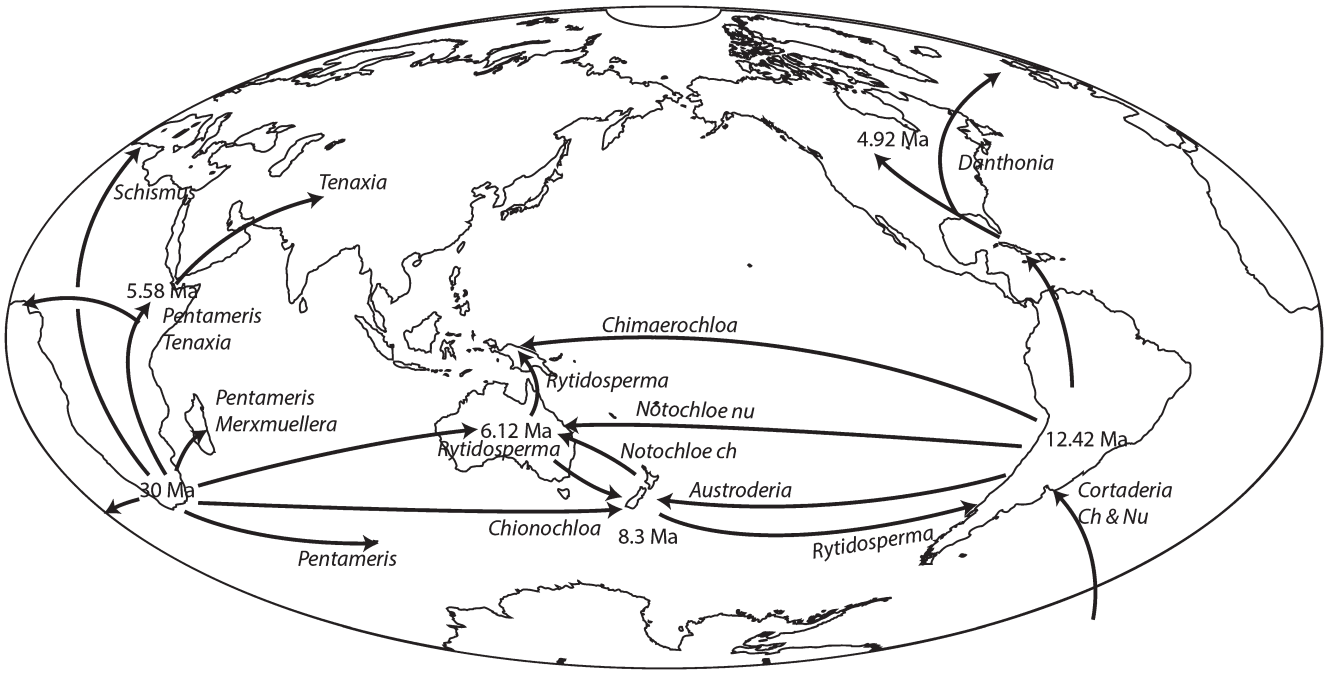

Fig. 3. Biogeographical history of Danthonioideae, showing the inferred dispersal routes, and the dated median age of the first radiations on each continent. Modified from Linder *et al.* (2013).

new habitats. The third line of evidence is the postulated rapid spread and wide distributions of ecologically key grass species.

During the Neogene, there were frequent trans-oceanic dispersal and global range expansions in several grass clades. For example, the Danthonioideae (280 spp.) likely originated in southern Africa in the Oligocene. From the Middle Miocene onwards the subfamily expanded its range, with minimally two dispersal events to South America, one to New Zealand, and one to Australia (Linder *et al.*, 2013) (Fig. 3). Multiple dispersal events took place from Australia to New Zealand, South America and New Guinea, and of the South American clade to North America, New Zealand, Australia and New Guinea. During the late Miocene, three clades also expanded from southern Africa to Madagascar, North Africa and the Mediterranean, and the Himalaya (Linder *et al.*, 2013). In many regions, local radiations resulted in significant increases in diversity (Linder *et al.*, 2014). Similar patterns are evident in several grass clades. In the Pooideae, the Loliinae (Festuca, Pooideae) probably originated in the Mediterranean in the mid-Miocene, and dispersed with numerous long-distance dispersal events across the Atlantic Ocean to the Americas, and from there expanded into a modern global distribution (Inda *et al.*, 2008; Minaya *et al.*, 2017). Similarly, *Hordeum* (also Pooideae) probably originated in the mid-Miocene in Asia, and also dispersed globally, with some back-dispersal and several hybridization events (Blattner, 2006; Brassac & Blattner, 2015). In the Stipeae, *Patis* and *Ptilagrostis* migrated from the Irano-Turanian region in Asia to North America during the late Miocene (Romaschenko *et al.*, 2014). Remarkably, many of these long-distance dispersal events are also associated with putative hybridization and plastid-capture events, suggesting even more frequent dispersal events (Blattner, 2006; Linder *et al.*, 2013; Romaschenko *et al.*, 2014; Brassac & Blattner, 2015).

Pan-tropical grass floras were transformed within a few million years from C_3 to C_4 dominance (Edwards *et al.*, 2010), and this also entailed a major re-organisation of tropical vegetation with a global reduction in forest extent and the origins of the savanna biome. However, the broad geographical dispersal of the major C_4 clades makes historical biogeographical reconstructions challenging, and the only estimated area of origin for a diverse C_4 lineage is Asia or Africa for the Chloridoideae (Bouchenak-Khelladi *et al.*, 2010; Peterson, Romaschenko & Johnson, 2010). There are numerous widely distributed species, of which some established their ranges during the Quaternary. The most studied is *Alloteropsis semialata* (R.Br.) Hitchc., with both C_4 and C_3 photosynthetic genotypes likely to have originated in the Zambesian region of Africa. The C_4 genotype evolved only in the late Pliocene, dispersing in the last 2.5 Myr from Africa through Asia to Australia, and southwards to southern Africa (Lundgren *et al.*, 2015). Further, *Themeda triandra* Forssk. (Andropogoneae) originated in Southeast Asia in the last 2.5 Myr and dispersed throughout Asia, to Australia and New Zealand around 1 Ma, while dispersing to Africa well within the last 1 Myr (Dunning *et al.*, 2017). *Themeda triandra* now occurs as far north as southern France and central Japan, throughout Africa, Asia and Australia and is often ecologically dominant. The genus *Themeda* contains 27 recognized species, and the range of *T. triandra* not only encompasses the

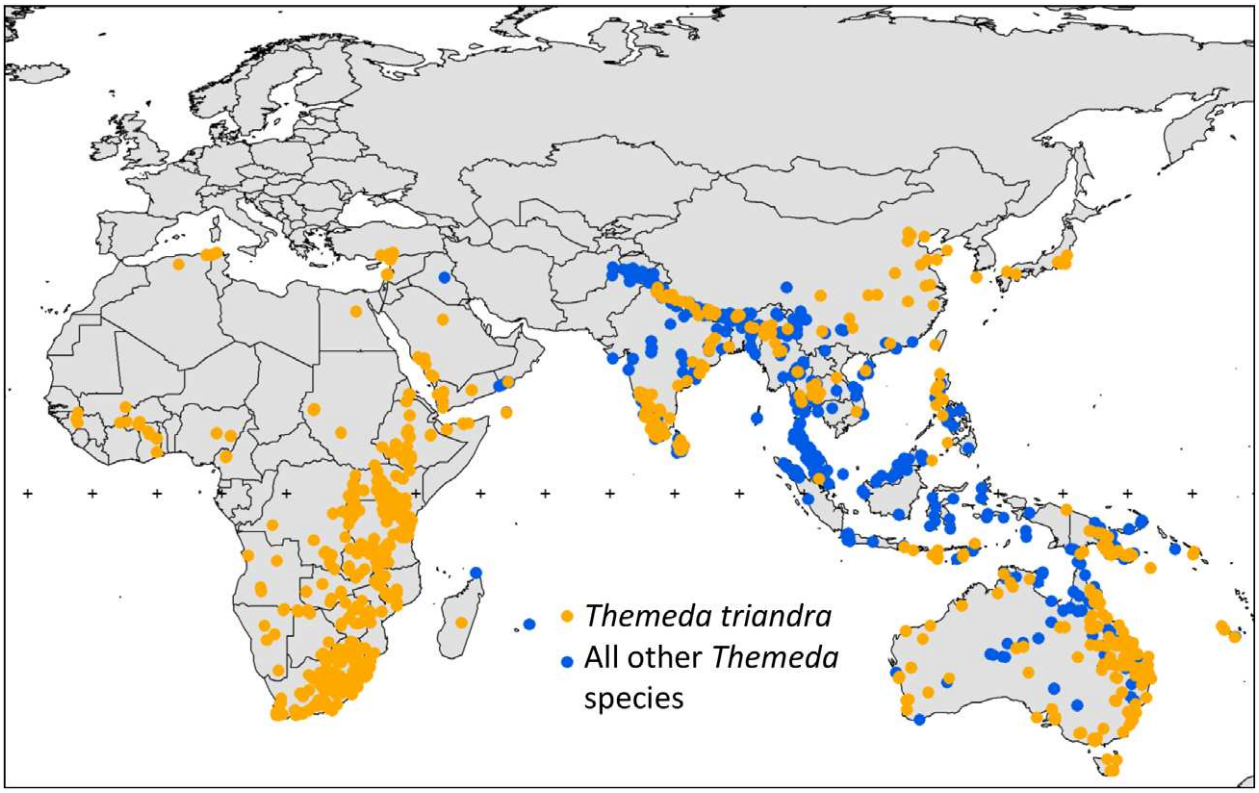

Fig. 4. Distribution range of *Themeda triandra* compared to that of the whole genus, demonstrating a pan-palaeotropical range. Data derived from Morales (2014) and Dunning *et al.* (2017).

geographic ranges of all other species, but also significantly extends the range of the genus as a whole (Fig. 4). There are also several cosmopolitan grass species [e.g. *Phragmites australis* (Cav.) Trin. ex Steud., *Heteropogon contortus* (L.) P.Beauv. and *Deschampsia cespitosa* (L.) P.Beauv.], but a critical evaluation of whether there are more widely distributed species in grasses than in other families is confounded by the absence of readily comparable data.

III. TRAITS THAT COULD FACILITATE INVASIVENESS

Successful invaders should (*i*) be good at dispersal (e.g. getting to new areas), (*ii*) be able to establish from small founding populations (genetically surviving bottlenecks and avoiding extinction due to stochastic events), (*iii*) survive, proliferate and spread in the new environment, and (*iv*) modify the new environment to make it more suitable for themselves and less suitable for other residents. Functions are the results of new traits or combinations of traits. The evolution of traits may be easier to trace than the evolution of functions (Fig. 5), as the latter may depend on the interaction of environment and trait. There are very few critical tests of trait–function relationships in the grasses, and much of the linkage proposed is consequently speculative (e.g. Table 2).

(1) Dispersal

Both trans-oceanic and trans-continental long-distance dispersal are obvious pre-requisites for effective palaeo-invasions. There is enormous variation in the grass dispersal unit (diaspore), and Davidse (1987) suggests that selection for effective dispersal might be one of the reasons for the rich diversity of grasses. The grass diaspore is either a whole or part of an inflorescence (Gibson, 2009). The basic organisational unit in grass inflorescences is the grass spikelet (Fig. 6C), a structure unique to the grasses. The spikelet consists of two basal bracts (lower and upper glumes), subtending one or more flowers. Each flower (Fig. 6B) consists of two basal bracts (lemma and palea, interpreted by Kellogg, 2015 as containing the outer perianth parts), 2–3 lodicules (probably modified inner perianth parts; Kellogg, 2015) and 3–6 stamens. Furthermore, the pseudomonomerous gynoecium (ovary with apparently just one carpel) forms a caryopsis [a single-seeded nut with ovary wall fused to the seed coat (Rudall *et al.*, 2005)]. This spikelet structure evolved at the common node of the Pharoideae and the rest of the grasses (Kellogg, 2000), and so is not ancestral to all grasses. Arber (1934) showed that the inflorescence of *Streptochaete*, the first diverging grass, does not conform to the model of a grass spikelet. In contrast to the spikelet, the pseudomonomerous gynoecium and caryopsis are synapomorphies of the grasses (Fig. 5), and could be interpreted as precursors to the spikelet as diaspore.

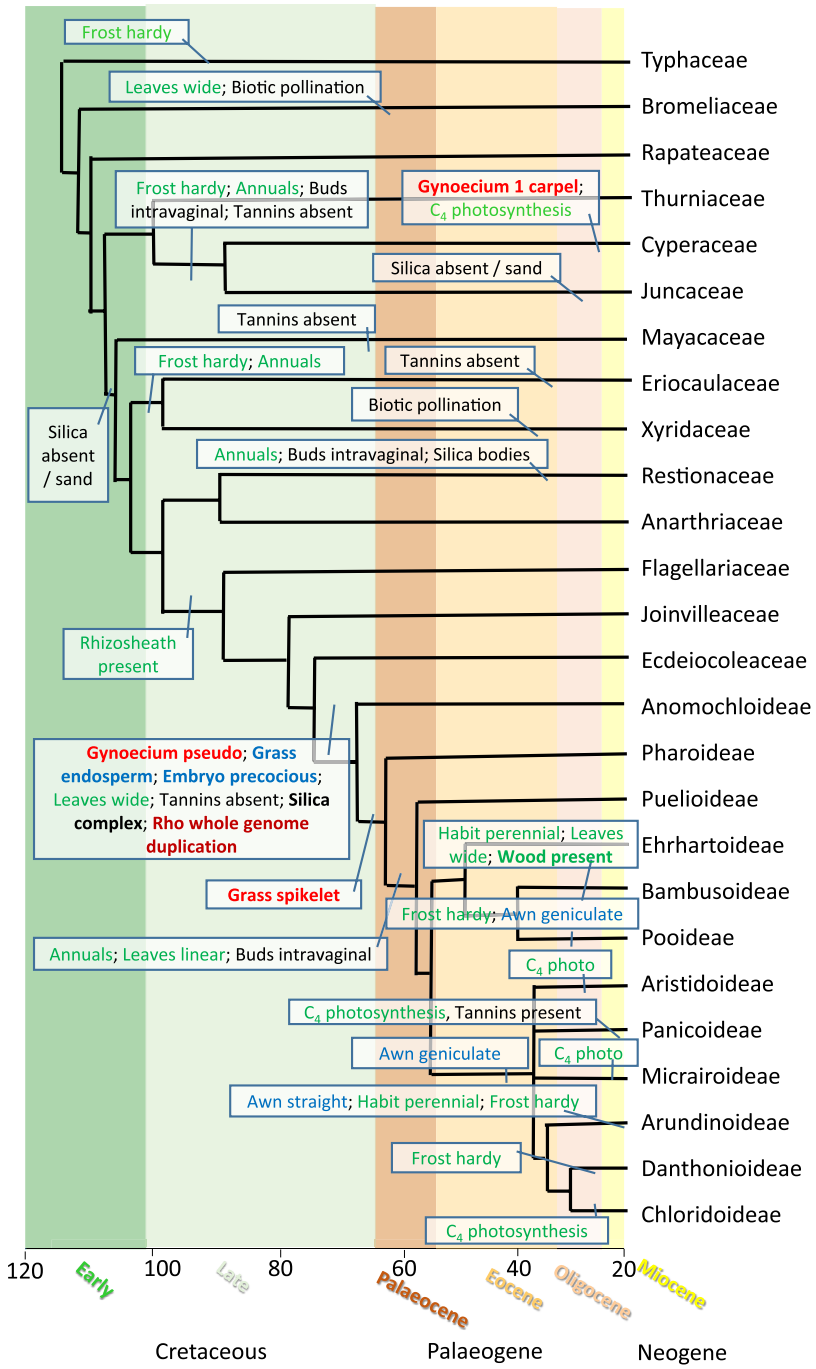

Fig. 5. Phylogeny of the Poales, based primarily on McKain *et al.* (2016) with details and ages added from Bouchenak-Khelladi *et al.* (2014). Note that the ages are approximate, as the errors around the age estimates are substantial. The traits are mapped over the phylogeny with fast parsimony implemented in CLADOS (Nixon, 1993); tips (e.g. families or subfamilies) were scored as present for a derived trait if it occurred scattered or commonly in the tip, and not necessarily common to all species (thus not all synapomorphies). The colour-coded ancestral states are listed below; derived states are shown in the figure. ***Dispersal traits (red)***: **gynoecium** three-carpellary; **spikelet** absent or not grass-like. ***Establishment traits (blue)***: **embryo** normal; **endosperm** not grasstype; **awn** none or straight (geniculate awns are variable in most clades with them). ***Ecological flexibility traits (green)***: **frost** intolerant; **photosynthesis** C_3 type (C_4 photosynthesis is not ancestral to any clade scored as C_4, but evolved numerous times); **habit** perennial (annual habit evolved many times in each tip with annuals); **leaves** narrow; **wood** absent; **rhizosheath** absent (rhizosheath presence is highly variable). ***Competitiveness traits (black)***: **buds** extravaginal (see Section III.4 for detailed discussion); **tannins** present; **pollination** wind (although the ancestral pollination mode of Poales is disputed, wind pollination was likely inherited in grasses); **silica** as simple bodies. ***Genetic traits (purple)***: **rho whole genome duplication** absent. Bold traits are unique transitions.

In most grass species the diaspore is the flower (caryopsis enclosed in the palea and lemma), but numerous modifications exist. Fleshy fruits [bacoid caryopses (Ruiz-Sanchez & Sosa, 2015)] are found in some forest bamboos. Similarly rare in the grasses are elaiosomes, containing oils attractive to ants, which develop largely from the pedicels of the flowers (Davidse, 1987). Depending on the positioning of the disarticulation between the diaspore and the rest of the plant, diverse elements may form the diaspore (Doust *et al.*, 2014). Disarticulation is rarely directly below the caryopsis; in such cases, only the caryopsis forms the diaspore. In most species, however, the disarticulation is on the floral pedicel, and the diaspore consists of the flower plus the upper part of the pedicel (the callus). In most Panicoideae the disarticulation is below the glumes and several sterile flowers may contribute to the diaspore (Doust *et al.*, 2014). In a few species, the disarticulation is below the inflorescence, which then forms a tumbleweed (Davidse, 1987). A major source of variation in the diaspore is the lemma and its awn. Both awns and lemma indumentum patterns are evolutionarily labile. The awns may be absent, hygroscopic, hooked, pointed, bristly or simple, and these might be the major adaptive structures that have facilitated a rich diversity of dispersal biologies in grasses. This range of diaspore types, and also including all floral parts in the fruit, is not unusual in the Poales, and is also found, for example, in Restionaceae (Linder, 1991) and Cyperaceae (Goetghebeur, 1998). Unique to grasses, though, is the awned lemma, and the complex indumentum of the lemma and the floral pedicel, referred to in the grasses as the callus.

Wind dispersal (anemochory), dispersal *via* animal coats (epizoochory), and after ingestion (endozoochory) are all reported in grasses. Anemochory is probably facilitated by long slender awns and small caryopses, as found for example in *Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn., but there is a dearth of experimental studies and critical observations. Epizoochory is an ancient dispersal syndrome in grasses, and Poinar & Columbus (1992) reported a spikelet associated with mammal hair from Eocene Dominican amber. Epizoochorous dispersal is facilitated by, *inter alia*, barbs and hooks on the lemmas and awns (Davidse, 1987). There are numerous reports of epizoochorous dispersal, e.g. *Themeda triandra* by Kenyan hares (Agnew & Flux, 1970), diaspores of numerous grass species in the wool of sheep in the South African Karoo (Milton, Siegfried & Dean, 1990), and *Stipa setacea* R.Br. in Australia (Arber, 1934). Bläss *et al.* (2010) suggest that it is a common dispersal mode of grasses found in Mongolia. Salt-marsh grass diaspores are common on waterbird feathers (Vivian-Smith & Stiles, 1994). Both endozoochory (deposited in dung) and epizoochory (found in the hair) were found for prairie grasses in bison (Rosas *et al.*, 2008). Rosas *et al.* (2008) did not locate a strong match to adaptations, but did find different profiles in the two dispersal modes. Endozoochory is associated with small, smooth, hard seeds or diaspores (Shiponeni & Milton, 2006) which protect the seed from the molar mill and during the passage through the gut. It seems likely that in most grasses the seed is ingested accidentally during grazing, consistent with Janzen's (1984) 'foliage is the fruit' hypothesis. At least in the Serengeti, endozoochory is an important dispersal mode in grasses (Anderson, Schutz & Risch, 2014). Some grass species can be dispersed by several means. We suggest that transformation of the spikelet, with its evolutionarily labile lemma as diaspore, may have been a key innovation in grasses. Surprisingly, there appears to have been no comparative or experimental work on the evolution and function of the grass diaspore.

(2) Establishment

Establishment includes not only the initial development of a dispersed seed into a sexually mature plant in a new habitat or continent, but also the medium-term success of subsequent generations (this conforms to the concept of 'naturalization' in plant invasion ecology; Richardson & Pyšek, 2012). The latter requires protection against the stochastic events that could eliminate small populations, as well as medium-term protection of the genetic diversity of the small, newly established populations. Effective establishment increases the proportion of dispersal events resulting in new populations. Several grass traits may contribute to establishment success. Some, like vegetative reproduction and wind pollination, are quite widespread in angiosperms. Below we focus on several that are peculiar to grasses.

(*a*) *Generation time and embryo structure*

Short generation times substantially increase the invasive potential of species. Firstly, if all else is the same, shorter generation times result in higher population growth rates, and high population growth rates are characteristic of successful invaders (Moles *et al.*, 2012). Such species are therefore more likely to be able to take advantage of rare or marginal spatio-temporal opportunities for population establishment. Secondly, early reproduction results in higher rates of seed production in the first years, thereby enhancing propagule pressure (Moles *et al.*, 2012). Thirdly, short generation time increases the possibility of rapid responses to directional selection. Consequently, short-generation species can develop a rapidly advancing and adapting front when matched with high rates of dispersal. Although there is no comprehensive review of grass generation time, and indeed very few published data, we suspect that grasses generally have short generation times compared to other Poales. For example, *Poa annua* L. can flower 6 weeks after germination (Cope *et al.*, 2009), and many Andropogoneae flower within 1–2 years after germination (Estep *et al.*, 2014). However, there are exceptions: bamboos, for example, take 3–50 years to flower (Arber, 1934; Franklin, 2004). We postulate that the short generation time found in many grasses may be due to the unusual embryo and reserve storage in grasses.

The grass embryo (Fig. 6A) is, in the context of monocots and in particular Poales, a remarkable innovation. In all other Poales the embryo consists of a disc of undifferentiated cells, which at germination differentiate into roots, shoots

Table 2. Summary of traits and functions associated with invasiveness in grasses; a tick indicates a postulated association between the trait (column) and the function (row). Traits and functions are explained in detail in Section III, where the arguments for the postulated associations are also presented

	Traits										
Function	Embryo	Diaspore/spikelet	Lemma awns present	C_4 photosynthesis	Sympodial growth form	Extravaginal buds	Intravaginal buds/tillering	Leaf tannins	Roots	Clonality	Polyploidy
Dispersal		✓	✓							✓	
Establishment	✓		✓		✓					✓	✓
Ecological flexibility: climate range				✓							✓
Ecological flexibility: habitat range					✓						
Competitiveness: fire survival					✓						
Competitiveness: grazing tolerance					✓	✓					
Competitiveness: productivity				✓					✓		
Competitiveness: flammability							✓	✓			

and leaves (Rudall *et al.*, 2005). In the grass seed, the embryo is already differentiated into a primary root, a shoot with leaf initials, and a haustorial structure (scutellum), resulting in a remarkably complex and variable structure (Fig. 6A) (Natesh & Rau, 1984; Gibson, 2009). Kellogg (2000) very appropriately regards the grass embryo as an example of heterochronic change, where either the embryo development was accelerated, or the seed ontogeny delayed. At germination the roots and shoots are ready to grow, and the scutellum is in place to absorb the nutrients from the endosperm. Such a precocious embryo may reduce the time it takes for the plant to be established. This could be the key innovation that allows flowering within 1 year of germination. Consequently, many grasses have the reproductive biology of annuals or biennials, and the persistence biology of perennials.

(*b*) *Polyploidy and apomixis*

Polyploidy is one of the traits associated with invasive species (Pandit, Pocock & Kunin, 2011; te Beest *et al.*, 2012), and polyploids are also more likely to survive and be ecologically successful if new niches are available (Van de Peer, Mizrachi & Marchal, 2017). This is corroborated by the link demonstrated for Danthonioideae between long-distance dispersal and polyploidy (Linder & Barker, 2014). One possible reason is that polyploidy reduces the effects of genetic inbreeding in small, establishing populations (Rosche *et al.*, 2017), thus increasing the amount of additive genetic variance. Diploids may lose much genetic diversity due to inbreeding during the first few generations after the establishment of new populations. A disadvantage of polyploidy is that it can lead to the breakdown of self-incompatibility. However, grasses have a unique S-Z two-locus gametic self-incompatibility system, which appears to be common to the whole family (Li *et al.*, 1997), and in which polyploids retain their self-incompatibility (Baumann *et al.*, 2000; Langridge & Baumann, 2008; Yang *et al.*, 2008). A second reason for the success of invading polyploids may be a result of wider ecological niches than in diploids (te Beest *et al.*, 2012). A third reason could be that polyploid grasses are often apomictic (Pullaiah & Febulaus, 2000), so leading to assured reproduction, while protecting the heterozygosity of the lineage.

Polyploidy, and especially allopolyploidy, is extremely common in the grasses (Kellogg, 2015). Hunziker & Stebbins (1987) noted that more than 80% of grass species have a (recent) polyploid history, compared to 25–30% for angiosperms in general (Van de Peer *et al.*, 2017). Furthermore, proportions of (neo-)polyploids in the grasses are higher than in any other large family, and all large genera have a majority of polyploids (Stebbins, 1985). Many polyploids appear to be allopolyploids, and this could indicate rampant hybridization. Estep *et al.* (2014) showed that allopolyploidy is extremely common in the Andropogoneae, indicating a link to the diversification of this important clade of savanna grasses.

(*c*) *Hygroscopic awns*

Hygroscopic awns (Fig. 6B, C) may help plant the caryopses, presumably in better microhabitats for germination and establishment than where the caryopsis landed (Peart, 1979; Peart & Clifford, 1987), thus increasing the proportion of dispersal events resulting in successful population establishment. Hygroscopic awns, which twist when the

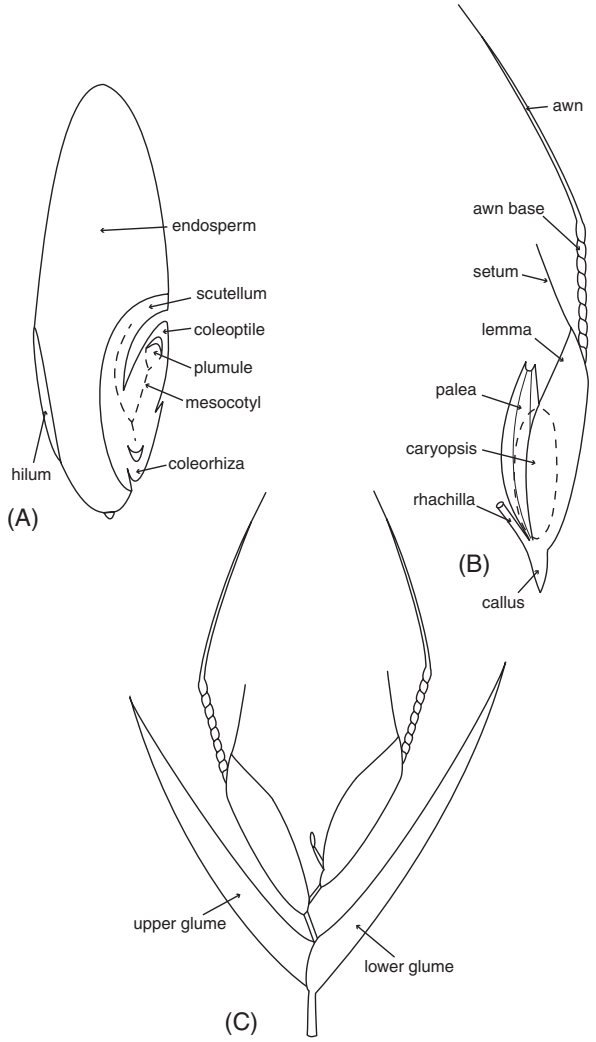

Fig. 6. Simplified diagrammatic illustration of grass diaspores. (A) Longitudinal section through the caryopsis. The hilum is the attachment of the seed wall. (B) One flower, with a two-keeled palea and three-awned lemma, the central awn hygroscopic with a twisted base. (C) Two-flowered spikelet. Drawn by Melanie Kleineberg-Ranft.

humidity changes, are unique to the grasses and are found in 199 genera in Panicoideae, Danthonioideae and Pooideae (Watson & Dallwitz, 1994, updated 2015). They have evolved several times and are evolutionary labile, thus are also readily lost (Humphreys *et al.*, 2011).

(3) Environmental flexibility

Although grasses occupy almost the complete range of angiosperm habitats (Fig. 1), the specialization of grass lineages into different environmental niches results in an even distribution in species richness from the equator to high latitudes (Visser *et al.*, 2012, 2013). Ecological specialists within these groups occupy a range of extreme environments, from aquatic habitats (e.g. the floating grass *Hygrooryza aristata* Nees) to hyperarid deserts (*Stipagrostis zitellii*; J. Léonard in White, 1983), high altitudes [*Pentameris minor* (Ballard & C.E.Hubb.) Galley & H.P.Linder may be the highest plant on Mt Kilimanjaro] to coastal dunes [e.g. marram grass, *Ammophila arenaria* (L.) Link], and deep shade of the forest understorey (e.g. *Oplismenus burmannii*) to sunny savanna (e.g. *Themeda triandra*). There are even several resurrection grass species from southern Africa (Gaff & Ellis, 1974) and Australia (Gaff & Latz, 1978). There are few habitats without grasses, such as marine and epiphytic habitats (although there are epilithic grasses). Grasses are rare in some biomes, such as tundra, sandy deserts, succulent thickets, dry forests and shrublands. In some densely forested biomes, such as evergreen montane forests, grasses occur in disturbed areas (e.g. *Chionochloa* in the New Zealand *Nothofagus* forests). Below we explore five trait-systems that likely contribute to this wide range of habitat tolerance. Such long-term evolutionary lability may be correlated with short-term plasticity, an attribute of successful invaders (Moles *et al.*, 2012). We expect that environmental flexibility may be predicted to be the result of trait diversity, rather than of any particular trait.

(*a*) *Frost tolerance*

Grasses probably evolved in a tropical, frost-free environment (Clayton, 1981; Edwards & Smith, 2010), and frost tolerance has evolved several times (Preston & Sandve, 2013). The largest frost-tolerant clade is Pooideae (Clayton, 1981), but the trait also evolved in the Danthonioideae (Humphreys & Linder, 2013), and other lineages, including *Alloteropsis* (Osborne *et al.*, 2008; Lundgren *et al.*, 2015), *Pennisetum* and *Cleistogenes* (Liu & Osborne, 2008). The biochemical basis of frost tolerance has been elucidated for the Pooideae (Sandve & Fjellheim, 2010; Sandve *et al.*, 2011; Vigeland *et al.*, 2013). Frost tolerance enables Pooideae to colonize the vast steppe regions, and is, at least in Danthonioideae, linked to significant range extension (Humphreys & Linder, 2013; Wüest *et al.*, 2015) during the cooling Neogene. Based on distributional data, frost tolerance is found in Cyperaceae, Juncaceae, Typhaceae, probably in Eriocaulaceae, Xyridaceae, but not in Restionaceae, Anarthriaceae, Ecdeiocoleaceae, Flagellariaceae, Joinvilleaceae, Thurniaceae, Bromeliaceae and Rapateaceae. Most likely frost tolerance evolved numerous times, not only in grasses but across the Poales (Fig. 5).

(*b*) *Photosynthetic mode*

The repeated shifts in photosynthetic mode from C_3 to C_4 (Christin *et al.*, 2008, 2009; Christin, Freckleton & Osborne, 2010) have allowed grasses to be highly productive over a wide climatic range (Long, 1999). C_3 photosynthesis is generally associated with cool growing seasons or humid conditions (thus temperate climates and shady tropical forests), and C_4 with hot, and often arid or dry, growing seasons (thus seasonally dry tropical climates) (Sage, 2004). The transitions from C_3 to C_4 photosynthesis within grasses were associated in 18 of 20 cases with a shift into a drier climate (Edwards & Smith, 2010), and C_4 lineages have

overall been more likely to transition from mesic to arid niches than C_3 groups (Osborne & Freckleton, 2009). In addition to its direct effects on plant productivity (Atkinson *et al.*, 2016), C_4 photosynthesis is also associated with a lower stomatal conductance than the C_3 type (Björkman, 1971) with potential benefits for plant hydraulics in open, sunny environments that cause high rates of evaporation (Osborne & Sack, 2012). The carbon-concentrating mechanism of C_4 plants means that, for a given investment in the carbon-fixing enzyme Rubisco, they achieve higher rates of photosynthesis across a range of temperatures (Long, 1999). Since Rubisco can account for 30% of leaf nitrogen in C_3 species, this underpins greater photosynthetic nitrogen-use efficiencies in C_4 than C_3 plants (Long, 1999). In Panicoideae lineages of C_4 grasses (including Andropogoneae), accelerated catalysis by Rubisco has further enhanced nitrogen-use efficiency (Ghannoum *et al.*, 2005). In combination, these traits give C_4 plants the potential to allocate larger proportions of plant nitrogen to roots in infertile habitats, and to greater leaf area development in fertile or disturbed habitats (Long, 1999). In grasses, C_4 photosynthesis is associated with approximately 50% greater allocation of growth to roots during plant establishment in comparison with the C_3 type, with important implications for rooting depth and access to water and nutrients (Atkinson *et al.*, 2016). In *Alloteropsis semialata*, C_4 plants allocate more growth to both below-ground storage and sexual reproduction than their C_3 counterparts, pointing to a shift in life-history strategy enabled by the greater carbon availability in the C_4 form (Ripley, Abraham & Osborne, 2008). Evidence therefore suggests that C_4 photosynthesis improves carbon-uptake efficiency with respect to limiting soil resources (especially water and nitrogen) across a range of habitats, giving grasses greater access to alternative developmental and life-history strategies than the C_3 type. In the case of *A. semialata*, these advantages probably enabled a rapid expansion of the ecological niche when the C_4 pathway evolved (Lundgren *et al.*, 2015).

(*c*) *Flexible growth forms*

The diversity of degrees of persistence of culms, and possibly aerial rhizomes, may allow grasses to develop growth forms that enable them to survive annual defoliation (such as in grasslands or highly seasonal climates), continuous defoliation [resulting in lawn grasses (Hempson *et al.*, 2015)], and competition with perennial vegetation such as heathlands (Linder & Ellis, 1990) or forest (e.g. bamboos). This may be related to the relatively labile shift between intra- and extravaginal innovation buds (Fig. 7A, B) – a clear distinction between intra- and extravaginal innovation buds is difficult in the other Poalean families (Fig. 5). With intravaginal buds, the tillers are adjacent and the plant forms a bunch grass. Extravaginal buds may lead to spreading rhizomes and to lawn grasses with well-spaced tillers (Fig. 7), although some extravaginal species may also form tussock grasses. Phenotypic plasticity is also common, with many grass species able to alter the height, angle, branching structure, and rooting characteristics of their culms depending on environmental conditions [e.g. facultative lawn grasses (Hempson *et al.*, 2015)].

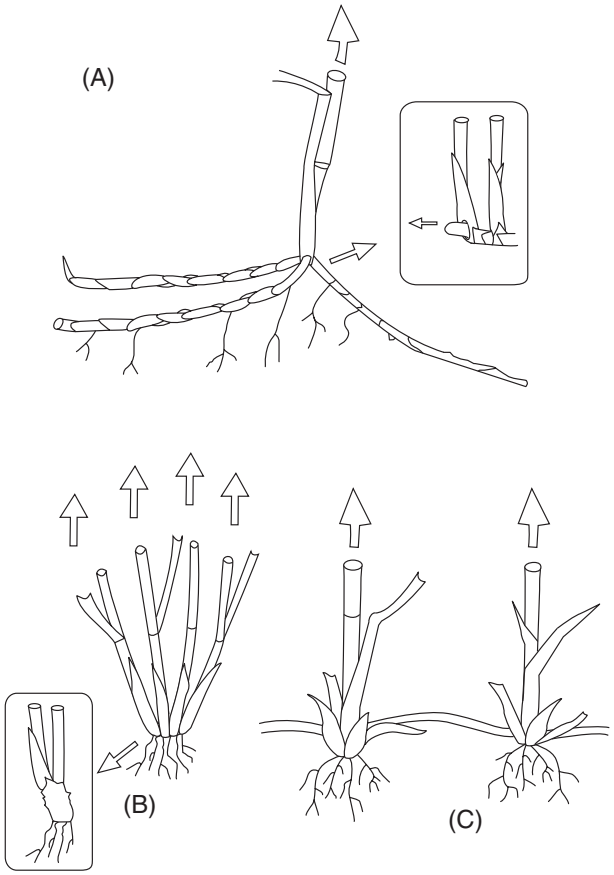

Fig. 7. Basic, simplified growth forms of grasses. (A) With long rhizomes and extravaginal innovation (in the insert). (B) Intravaginal innovation, with the tillers tightly bunched, forming a bunchgrass (inset illustrates intravaginal innovation). (C) Plants with stolons, which spread usually on the ground surface and 'plant' new tillers or tufts. The arrows indicate where flowering culms were cut. Drawn by Melanie Kleineberg-Ranft.

Bamboos compete successfully with forest trees in aseasonal climates by developing a certain woodiness (Clayton, 1981) (albeit without secondary thickening). The plants persist over decades as dense stands in forest. At the other extreme are annuals, where the species are present only during the rainy season, and so avoid the dry or hot season, a strategy suitable for predictable seasonal climates (Humphreys & Linder, 2013).

The hemicryptophyte growth form (buds at or near the soil surface) is common in grasses. This means that even perennial grasses do not need to retain aboveground biomass through unfavourable conditions, and can regrow from the base after defoliation. Ripley *et al.* (2015) showed that fire-adapted species recover all their biomass within 60 days of defoliation, and other grass species recovered some 50% of their biomass in this period. This may be a key innovation for seasonal drought, fire, heavy grazing or cold: effectively having an annual above-ground architecture on a perennial plant.

(*d*) *Stomata and water relationships*

In grass stomata the dumbbell-shaped guard cells are flanked by two subsidiary cells, thus the whole stomatal complex includes four parallel cells (Hetherington & Woodward, 2003). This paracytic stomatal complex is typical of the Poales–Commelinales–Zingiberales clade (Rudall, Chen & Cullen, 2017). In grasses a rapid stomatal response to changing moisture regimes has been demonstrated (numerous references in Franks & Farquhar, 2007). Franks & Farquhar (2007) demonstrated that in *Triticum aestivum* L. stomatal opening required a massive contraction in the subsidiary cells, and they postulated that this was achieved by shifting potassium ions between the guard and the subsidiary cells. The resulting stomata are both larger and can respond more rapidly to changing environmental conditions. Raissig *et al.* (2017) identified the genetic regulators of grass subsidiary cells, and used these to generate mutant grasses with 'normal' two-celled stomata. The wild type of *Brachypodium distachyon* (L.) P.Beauv. (with four-celled stomata) grew faster, the stomata opened wider, and responded more rapidly to changing light intensity, than the mutants with 'normal' two-celled stomata. Thus, the wild-type phenotype leads to a higher photosynthetic rate at a smaller water loss. These advantages are further fine-tuned by differences in stomatal size (affecting the closure speed), leaf width (influencing the rate at which leaves can roll up) and stomatal densities, among arid and mesic habitat lineages (Liu & Osborne, 2015). Hetherington & Woodward (2003) suggested that these efficient stomata may have contributed to the grass success in the aridifying Neogene world, giving the grasses a competitive edge in a water-limited environment. However, it is not known whether the paracytic stomata in the other commelinid families show a similar physiological pattern.

(*e*) *Rooting systems and resource competition*

Grasses grow in the complete range of 'soil' environments, from standing water to Sahara sand. Although grasses lack unique root innovations, this remarkable range may be achieved by variation in the rooting architecture, the presence of mycorrhizae, and the development of a rhizosheath (sandsheath). According to Hartnett *et al.* (2013) these three mechanisms complement each other in the southern African semi-desert Kalahari: mycorrhizal associations (which were found in all investigated Kalahari grasses) are more common and so probably more important in infertile soils with good rainfall. A finely divided root system is better developed in fertile, arid soils. Consequently, the degree of root branching varies inversely with the degree of mycorrhizal association. Finally, rhizosheaths (thick sandy sheaths held together by hair-like epidermal structures and mucilage that coat the full length of every root on the plant) are better developed in sandier soils in more arid conditions than in fine-textured soils in wetter conditions.

Grasses generally produce a dense mass of finely divided roots (Kutschera & Lichtenegger, 1982; Kellogg, 2015), and investigations in a seasonal savanna show that grass roots tend to concentrate in the top few centimetres of soil, which makes them effective at intercepting incoming water and accessing available nutrients (Scholes & Walker, 1993; February & Higgins, 2010). This root morphology may be linked to having an expendable above-ground architecture, which does not require an extensive deep root system to maintain subaerial biomass during unfavourable conditions (Nippert *et al.*, 2012).

Rhizosheaths probably improve water movement across the soil–root interface (Hartnett *et al.*, 2013), but they have also been linked to improved P uptake. These structures have been documented for the Australian Restionaceae, Cyperaceae, Anarthriaceae and Ecdeiocoleaceae (Pate & Dixon, 1996; Pate & Meney, 1999), and also occur in the African Restionaceae (H.P. Linder, personal observations). They are widespread in the grasses, and Bailey & Scholes (1997) recorded them from most species in the Kalahari. Absence of rhizosheaths in the early-diverging grass lineages, as well as in the Bambusoideae, may be due to their absence from arid, sandy habitats.

(4) Ecological competitiveness

Ecological competitiveness includes the ability, first, to usurp resources from other species, and, second, to transform the environment biotically. Consequently, habitats invaded by grasses become more hostile for other plants, particularly restricting the growth and recruitment of woody plants. Anthropocene grass invasions provide convincing evidence of the speed of biotic feedbacks (Gaertner *et al.*, 2014). D'Antonio & Vitousek (1992) suggest that invasive grasses transform environments by outcompeting tree and shrub seedlings for light, water and nutrients, as grasses can form a dense sward (Bond, 2008; February *et al.*, 2013; but also see O'Connor, 1995 for an exception). Environmental transformation also results from biotic feedbacks that engender chronic disturbance (Brooks *et al.*, 2004). First, grasses can increase fire frequency (D'Antonio & Vitousek, 1992; D'Antonio, Stahlheber & Molinari, 2011). Fire exclusion demonstrates that, without fire, grasses are often out-competed by tree saplings (Bond, Midgley & Woodward, 2003; Bond, Woodward & Midgley, 2005; Bond, 2008; Scheiter *et al.*, 2012). Second, increased plant consumption and trampling by mammalian herbivores acts to keep systems open (Clayton, 1981; Charles-Dominique *et al.*, 2016). Both fire and grazing are facilitated by spatially continuous populations of grasses (Archibald & Hempson, 2016). Wind pollination may be an essential trait for very large, contiguous, populations. Wind-pollinated plants cannot be pollen limited in open habitats, whereas pollinator saturation has been demonstrated for biotically pollinated species, at least for cultivated fields (Holzschuh *et al.*, 2016).

(*a*) *Flammability and fire-tolerance*

Leaf chemistry, and plant architecture, as well as rates of growth and decomposition alter the flammability of grasses, thereby influencing fire spread and frequency (Fernandes

& Cruz, 2012; Schwilk, 2015). Generally, plants with high leaf C:N ratios (tannins) and volatile oils and resins ignite more readily (Belcher *et al.*, 2010; Pausas *et al.*, 2016), and fine leaves arranged with a low bulk density can increase flammability (Schwilk, 2003).

Grasses, like all Poales and most monocots, have no woody tissue [except, arguably, the woody bamboos (Clayton, 1981)]. The absence of woody tissue reduces the energetic costs of resprouting post-fire, contrary to the situation in most eudicots and all trees. It also means that a high proportion of carbon is invested in photosynthetically active tissue; this enables grasses to regain productivity rapidly after defoliation. The grass growth form is thus well adapted to pulsed resource availability (Bond, 2008) such as seasonal rainfall and frequent fire. The common hemicryptophyte habit sees perennating buds buried, either in the soil or in a dense tussock base, where they are protected against fast-burning fires, typical of grasses (Pausas, Keeley & Schwilk, 2017). The rates of curing and decomposition affect how much dead plant material is available at any time. Andropogoneae, and a few other clades, have a high tannin content (Ellis, 1990) and these are thought to slow decomposition. Curiously, tannins or tannin-like substances are almost universally present in the Poales, but are absent in many grass lineages (Ellis, 1990), and the presence of tannins in the Andropogoneae is almost certainly a secondary gain.

The composition of ground-layer species of savannas is influenced by fire frequency, indicating that some species (mostly Andropogoneae) cope better with a high fire frequency (Visser *et al.*, 2012; Forrestel, Donoghue & Smith, 2014). These fire-tolerant species commonly have a caespitose architecture where buds are nested about dense leaf bases. Evidence demonstrates variability both in flammability (Simpson *et al.*, 2016) and rates of resprouting post-fire (Ripley *et al.*, 2015) of co-occurring grass species.

(*b*) *Grazing*

Grasses respond to grazing both with defences and with a biology enabling survival in the face of constant defoliation. The remarkably diverse silica bodies in the epidermal short cells (Metcalfe, 1960) are usually interpreted as herbivore defence (Mithofer & Boland, 2012), and may operate by abrading the chewing apparatus, or by diverse other means (Hunt *et al.*, 2008). Although silica sand is common in the Poales, and much simpler silica bodies occur in some Restionaceae and Thurniaceae (Cutler, 1969), complex silica bodies, with a wide range of shapes, are unique to grasses. Similarly, the presence of tannins in Andropogoneae (Ellis, 1990) could be interpreted as defence. Finally, C_4 grasses may have a lower digestibility than C_3 grasses, due to a higher fibre content (Gibson, 2009).

Nevertheless, the ecological dominance of highly palatable grass species is generally maintained by heavy grazing (McNaughton, 1979). Arber (1934) suggested that grasses were well adapted to survive grazing due to a tillering habit and the ability of the leaves to elongate from the base. Grazing tolerance is also associated with a high investment in below-ground reserves, growth forms which enable plants to retain leaves close to the ground, innovation buds below the soil surface, and strong root systems preventing uprooting (Diaz *et al.*, 2007). Consequently, caespitose bunchgrasses (Fig. 7B) are less resistant to grazing than rhizomatous or stoloniferous grasses (Fig. 7A, C) (Mack & Thompson, 1982; Coughenour, 1985).

IV. TRAIT EVOLUTION AND SEQUENTIAL INVASIONS

The grasses most likely started their evolutionary history in the shady understorey of forests, and diversified in this habitat through the first 20 Myr. Although the evidence is sparse, there is some indication of grassy patches in these Palaeogene (65–34 Ma) forests (Morley, 2000; Strömberg, 2011). They inherited wind pollination, a sympodial growth form and paracytic stomata, and the ancestral grasses already had a precocious embryo and large starch reserves (Fig. 5). The large embryo and starch reserves may have facilitated establishment in dark forest understorey, and the four-celled stomatal apparatus, responding rapidly to changing light, could also initially have been advantageous for exploiting light patches in forests. Defence against herbivory appears to have shifted from tannins in the rest of the Poales, to silica bodies in the grasses. The role of whole genome duplications (WGDs) in the evolution of these traits is still unclear. There is evidence for three WGDs in the grass genome. Their phylogenetic placement was explored by McKain *et al.* (2016): the 'tau event' probably occurred early in monocot evolution, between the divergence of the Alismatales and Asparagales; the 'sigma event' occurred after the Poales–commelinid split; and the 'rho event' coincided with the origin of the grasses. *Rho* has been linked to a change in the starch biosynthesis process (Comparot-Moss & Denyer, 2009), and has also been linked to duplicated MADS-box genes (a conserved sequence motif) which might be associated with the evolution of the spikelet structure (Preston & Kellogg, 2006).

The initial shift into open habitats could be as old as the common node of the BEP and the PACMAD clades (Osborne & Freckleton, 2009), dated to the early Eocene, and linked to the evolution of the tillering habit and to tussock formation (possibly a fire adaptation) and narrow leaves (possibly a drought adaptation). The three basal lineages in the grasses are all extravaginal (H.P. Linder & C.E.R. Lehmann, personal observations), so irrespective of the interpretation of the position of the innovation buds in the other poalean families, there is a shift from extra- to intravaginal at the common ancestor of the BEP–PACMAD clade (Fig. 5).

The subsequent evolutionary history of grass may be interpreted as four invasions. The first is the bamboo (re-)invasion of tropical forests; this is correlated with the evolution of a woody habit. We do not explore this invasion in detail, but suggest that a further key innovation may be semelparity, with delayed flowering. The mechanisms by which bamboos

maintain massive stands in the absence of fire deserve more attention. The second is the Oligocene–Early Miocene C_3 grass invasion into woodlands, which is known only from the fossil record. It is not clear which clades contributed to this woodland invasion, and consequently it is difficult to determine the facilitating traits. The third is the spectacular late Miocene–Pliocene invasion by the C_4 grasses (Edwards *et al.*, 2010) in the tropics, largely by Andropogoneae. These presumably replaced pre-existing C_3 grasses, and possibly also the associated grassy woodlands (Retallack, 1992). Andropogoneae have a suite of innovations that might increase burning frequency: tannins, which slow leaf decay rates and cure rapidly, and C_4 photosynthesis with high nitrogen-use efficiency, which maximizes productivity in high-light, seasonally moist, and infertile soil environments. The fourth invasion was by the frost-tolerant Pooideae into the northern steppes, during the Eocene–Oligocene transition (Sandve & Fjellheim, 2010). The Pooideae invasion is matched in the Southern Hemisphere by the cold-tolerant Danthonioideae, these have been dated to the late Miocene and Pliocene (Linder *et al.*, 2013), but no supporting fossil evidence is available.

The current success of the grasses is most likely the result of a complex set of traits, which have accumulated throughout the history of the Poales. The first stage involved dispersal/establishment traits and stomata, which could be interpreted as allowing grasses to exploit ephemeral forest gaps. The second set of traits dealt with surviving grazing, and were probably associated with the Miocene woodland invasion. Finally, fire traits fuelled the invasion of C_3 grasslands and woody ecosystems by C_4 grasses. The inherited grazing traits allowed the development of massive herbivore biomass, and the dispersal/establishment traits spread these new grasses around the planet in the tropics. Such an accumulation of traits, gradually building a set of functionalities that enhance dispersal, establishment, etc., might be a common feature of all evolutionarily successful clades. The cumulative effect of these traits is that the efficacy of the grasses as colonizers gradually improved through the Cenozoic. These traits result in the grasses being remarkably polymorphic in their dispersal biology, to be able to survive founder events both genetically and in terms of their population biology, being able to adapt to most habitats open to angiosperms on Earth, and being able to outcompete (over a large part of the planet) the other plants in those environments. This makes them the invaders from hell, bringing fire and hungry herbivores in their baggage.

V. CONCLUSIONS

(1) The modern success of the grasses (global distribution, presence in almost all angiosperm habitats, dominance over a large portion of the vegetated earth, and high species richness) can be interpreted as the result of increasingly effective waves of 'invasions', resulting from the evolution of appropriate traits.

(2) Grasses probably evolved in the late Cretaceous, with traits such as precocious embryos and large starch reserves which may have allowed rapid establishment in rainforest light gaps. The early evolution of the spikelet, and the floret with its awned lemma as dispersal unit, may have facilitated a switch between epi- and endozoochory, and facilitated rapid dispersal. This, together with the sympodial growth form and absence of above-ground woody investment, may have led to the first grassy patches in the Eocene and Oligocene, although it is not clear what grass clades formed these.

(3) In the second round of grass expansion and invasion the C_3 grasses in the early and middle Miocene probably formed a grassy woodland, and may have been facilitated by the tillering habit, which is associated with fire survival. The taxa involved are still enigmatic.

(4) The most recent (late Miocene–Pliocene) round of invasions led to the formation of the C_4 savannas in mesic tropical regions, largely involving the Andropogoneae. A central innovation is thought to have been the evolution of C_4 photosynthesis, but this happened almost 20 Myr earlier. A second innovation may have been the (re)-evolution of tannin synthesis. Both these traits may result in more frequent fires, due to a greater productivity of flammable biomass, and the preservation of this litter.

(5) In both Miocene and Pliocene invasions, the effective dispersability (thus not only the ability to cross wide barriers such as oceans, but also to establish viable populations), may have been central, facilitating a global response to global climate change. The traits facilitating this (a precocious embryo and the awned lemma dispersal unit) evolved earlier.

(6) The physiological ability of the grasses to survive in such a very wide range of habitats increases the possibility that, in some of them, the climatic conditions which they can exploit (such as strongly seasonal climates) may evolve, allowing them to become dominant within those ecosystems. Their high effective dispersability then allows them to become established in equivalent biomes on all continents.

(7) The invasion paradigm ('the Viking Syndrome') is a productive paradigm under which to explore the reasons for the success of grass. The predictions from the Viking syndrome might be interesting to explore for other highly successful, species-rich, clades.

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